



McDONALD INSTITUTE CONVERSATIONS

Far from the Hearth

Essays in Honour of Martin K. Jones

Edited by Emma Lightfoot, Xinyi Liu & Dorian Q Fuller

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(Above) Martin Jones at West Stow, 1972 (with thanks to Ian Alister, Lucy Walker, Leonie Walker, and West Stow Environmental Archaeology Group); (Below) Martin Jones in a millet field, Inner Mongolia, 2010. (Photograph: X. Liu.)





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Published by:

McDonald Institute for Archaeological Research
University of Cambridge
Downing Street
Cambridge CB2 3ER
UK
(0)(1223) 339327
info@mcdonald.cam.ac.uk
www.mcdonald.cam.ac.uk



McDonald Institute for Archaeological Research, 2018

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ISBN: 978-1-902937-87-8

Cover image: *Foxtail millet field near Xinglonggou, Chifeng, China, photographed by Xinyi Liu, September 2014.*

Edited for the Institute by James Barrett (*Series Editor*) and Anne Chippindale.

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Acknowledgements

The initial idea of editing this volume grew out of a conversation between Xinyi Liu and Graeme Barker at St John's College, Cambridge in June 2016. The editors subsequently discussed the provisional layout of the volume. By April of the following year, our list of agreed contributors was complete. Abstracts followed, and the chapters themselves soon after. First of all, the editors would like to pay tribute to our 36 authors, whose excellent work and timely contributions made it all possible.

For the last two-and-a-half years, the volume has been known as 'Fantastic Beasts' in order to keep it a secret from Martin. As we enter the final stage, we wish to extend our thanks to all who have ensured Martin remains blissfully unaware, including Lucy Walker, and we offer her our sincere thanks. We are extremely grateful to Harriet Hunt, Diane Lister, Cynthia Larbey and Tamsin O'Connell, who are kindly

organizing the gatherings to mark Martin's retirement and the publication of this volume.

With respect to the volume's production, we would like to thank the McDonald Institute for Archaeology Research for financial support. The McDonald Monograph Series Editor James Barrett oversaw and encouraged all aspects of this project, and we offer him sincere thanks. We would also like to acknowledge the support of Cyprian Broodbank, not least for allowing us to host the workshop at the institute, but also for his encouragement throughout all phases of the volume's implementation. Particular thanks must go to several key individuals: Anne Chippindale, Ben Plumridge, Emma Jarman, Simon Stoddart and Samantha Leggett. Finally, we are also grateful to the anonymous reviewers who recommended changes that have greatly enhanced the final version of this volume.

*Xinyi Liu, Emma Lightfoot and Dorian Fuller
August 2018*

Foreword

The 28-year term of Martin Jones as the first George Pitt-Rivers Professor of Archaeological Science witnessed, and in part created, a transformation in the fields of environmental and biomolecular archaeology. In this volume, Martin's colleagues and students explore the intellectual rewards of this transformation, in terms of methodological developments in archaeobotany, the efflorescence of biomolecular archaeology, the integration of biological and social perspectives, and the exploration of archaeobotanical themes on a global scale. These advances are worldwide, and Martin's contributions can be traced through citation trails, the scholarly diaspora of the Pitt-Rivers Laboratory and (not least) the foundations laid by the Ancient Biomolecules Initiative of the Natural Environment Research Council (1989–1993), which he chaired and helped create. As outlined in Chapter 6, Martin's subsequent role in the bioarchaeology programme of the Wellcome Trust (1996–2006) further consolidated what is now a central and increasingly rewarding component of archaeological inquiry. Subsequently, he has engaged with the European Research Council, as Principal Investigator of the Food Globalisation in Prehistory project and a Panel Chair for the Advanced Grant programme. As both practitioner and indefatigable campaigner, he has promoted the field in immeasurable ways, at critical junctures in the past and in on-going capacities as a research leader.

The accolades for Martin's achievements are many, most recently Fellowship of the British Academy. Yet it is as a congenial, supportive—and demanding—force within the Pitt-Rivers Laboratory that the foundations of his intellectual influence were laid. Here, each Friday morning, the archaeological science community would draw sticks to decide who would deliver an impromptu research report or explore a topical theme. Martin is among the most laid-back colleagues I have worked with, yet simultaneously the most incisive in his constructive criticism. As a provider of internal peer-review he was fearless without being unkind. The themed Pitt-Rivers Christmas parties were equally impactful—on one occasion Alice Cooper appeared, looking ever so slightly like our professor of archaeological science.

Martin's roles as a research leader extended to several stints as head of the Department of Archaeology, chairing the Faculty of Archaeology and Anthropology and serving as a long-term member of the Managing Committee of the McDonald Institute for Archaeological Research. Having started his professional career as an excavation-unit archaeobotanist in Oxford, he was a long-standing proponent of the highly successful Cambridge Archaeological Unit. In the wider collegiate community, he is a Fellow (and was Vice-Master) of Darwin College and was the staff treasurer of the Student Labour Club. In all roles he fought valiantly and often successfully for the interests of his constituency. His capacity to fight for deeply held priorities while recognizing the value of diverse perspectives was of utmost importance. His nostalgic enthusiasm for the debate with archaeological science that was engendered by the post-processual critique is one signal of an underlying appreciation of plurality. His active support for the recent merger of the Divisions of Archaeology and Biological Anthropology, within our new Department of Archaeology, is another. As a scientist (Martin's first degree, at Cambridge, was in Natural Sciences) he values the peer-reviewed journal article above all scholarly outputs, yet has authored as many highly regarded books as a scholar in the humanities. His *Feast: Why humans share food* has been translated into several languages and won Food Book of the Year from the Guild of Food Writers. He views academia and society as a continuum, campaigning for archaeobotanical contributions to global food security (e.g. by promoting millet as a drought-resistant crop) and working with world players such as Unilever to encourage archaeologically informed decisions regarding food products.

That Martin's achievements and influence merit celebration is clear. That his colleagues and students wish to honour him is equally so. Yet does the McDonald Conversations series publish *Festschriften*? This is a semantic question. As series editor I am delighted to introduce a collection of important papers regarding the past, present and future of archaeobotany, representing its methodological diversity and maturity. That this collection concurrently pays respect to a treasured colleague is a very pleasant serendipity.

Dr James H. Barrett

Chapter 14

A World of C₄ Pathways: On the Use of $\delta^{13}\text{C}$ Values to Identify the Consumption of C₄ Plants in the Archaeological Record

Emma Lightfoot, Xinyi Liu & Penelope J. Jones

Introduction

Most palaeodietary isotope studies, our own included, rely on the assumption that the C₄ signal detected in human skeletal remains reflects human and animal consumption of one or two major C₄ crops—usually millets (a group of small-grained taxa including *Setaria* and *Panicum*) in Eurasia or maize (*Zea mays*) in the Americas—rather than other C₄ or CAM plant species. This assumption is problematic, as stable isotope analysis can only distinguish between photosynthetic pathways; it does not comment on the species consumed. Nevertheless, many studies (again, our own included) have not adequately considered whether or not C₄ or CAM plants other than the major crop species may have been available for human and/or animal consumption. This paper calls for greater consideration in palaeodietary analysis of the potential for C₄ and CAM plant consumption beyond these major crops through an assessment of edible C₄ and CAM plants that are currently available in the region. Importantly, this requires assessing which C₄ or CAM plants are edible not only to humans, but also to any animals which may themselves have entered the human food chain. While the question of human consumption may be approached by paleoethnobotanical survey, determining the possibility of animal consumption is conceptually more challenging.

To build our case, we provide three regional case studies where we consider C₄ and CAM plant availability: Sicily, Italy; Haryana, India; and the south coast of Peru. These case studies have been selected to represent different environmental conditions, which are likely to have different proportions of C₃, C₄ and CAM plants available for human and animal consumption. They have also been selected to illustrate different methodological approaches to the problem of C₄ plant consumption, with the former two drawing on literature reviews undertaken by the authors,

while the third, taken from the published literature, uses direct isotopic analysis of plants collected in the field. Armed with this knowledge, we then consider how best one can use human and animal $\delta^{13}\text{C}$ values to identify and evaluate C₄ consumption in the archaeological record.

Background

Photosynthetic pathways

Photosynthesis is the process by which plants convert light energy to chemical energy by synthesizing sugars from carbon dioxide and water. There are three main types of photosynthesis, C₃, C₄ and CAM, which use different mechanisms to take in carbon dioxide from the atmosphere. Palaeodietary stable isotope analysis relies on the fact that these mechanisms discriminate to different degrees against isotopically heavy carbon dioxide (that is, carbon dioxide that incorporates carbon-13, ^{13}C ; e.g. O'Leary 1981). This means that the resulting plant tissues have stable isotope ratios that are different (i.e. fractionated) both from the isotopic ratio of the source carbon dioxide and from each other.

The mechanisms and differences between C₃, C₄ and CAM photosynthesis have been discussed in detail elsewhere and the reader is referred to Farquhar and colleagues (1982), Farquhar (1983), Osborne and Beerling (2006) and Sage and colleagues (2011) for a full discussion. In brief, the carbon-isotope value of C₃ plants is largely controlled by the diffusion of carbon dioxide through the stomata and the action of various enzymes, including Rubisco (Farquhar *et al.* 1982). C₄ photosynthesis evolved multiple times as a mechanism to increase the efficiency of Rubisco at higher temperatures by using a carbon-dioxide pump to concentrate the carbon dioxide around Rubisco before C₃ photosynthesis occurs (Farquhar 1983; Osborne & Beerling 2006). In contrast to C₃ and C₄ plants, CAM plants primarily take up carbon dioxide

at night, which reduces the rate of transpiration and allows them to live in some of the most water-stressed environments on Earth (Heyduk *et al.* 2016).

The vast majority of plants in the world use the C_3 photosynthetic pathway. C_3 plants represent 95 per cent of the world's plant biomass (Still *et al.* 2003), including most human and animal plant foods such as wheat, barley, rice, potatoes, fruits and vegetables. C_4 plants are mainly tropical grasses, but this group includes a small number of important food crops: most notably the millets, maize, sugarcane and sorghum (Sage *et al.* 1999). CAM plants are mainly succulents such as cacti (Silvera *et al.* 2010) and are hence rarely considered in the archaeological literature; nevertheless some CAM plants (such as pineapple) can be consumed.

Because the three different photosynthetic pathways discriminate against heavy carbon dioxide to different degrees, plants belonging to each pathway can be identified based on their carbon-isotope ratios (expressed as $\delta^{13}C$ values in units of per thousand: ‰). C_3 plants have $\delta^{13}C$ values between -35 and -21 ‰, C_4 plants between -20 and -6 ‰, and CAM plants between -33 and -14 ‰ (Bender *et al.* 1973; O'Leary 1988; Smith & Epstein 1971). By analysing the carbon isotope ratios of plant tissues, it is therefore straightforward to distinguish between C_3 and C_4 photosynthetic pathways—although identifying CAM plants in this way can be problematic due to their wide range, which overlaps with both C_3 and C_4 plants. Where assessing a plant's photosynthetic pathway based on its isotopic signature alone is not feasible or appropriate, an alternative approach is to identify photosynthetic pathways based on the anatomical features associated with C_4 and CAM photosynthesis.

Photosynthesis and archaeology

Identifying the photosynthetic pathways of plants in the human food chain has long been a concern of archaeologists. This interest stems in part from the importance of C_4 plants and their introduction to the food chain to some key transitions in human history: most notably the emergence of agriculture in the Americas (maize: e.g. Vogel & van der Merwe 1977), parts of China (foxtail and broomcorn millet: e.g. Zhao 2011), parts of Africa (sorghum, finger millet and pearl millet, *Sorghum bicolor*, *Eleusine coracana* and *Pennisetum glaucum*, respectively: e.g. Giblin & Fuller 2011; Manning *et al.* 2011), and parts of India (bristly foxtail, yellow foxtail, little, kodo and browntop millet, *Setaria verticillata*, *Setaria pumila*, *Panicum sumatrense*, *Paspalum scrobiculatum* and *Brachiaria ramosa*: e.g. Fuller 2006). In other contexts, there are also interesting archaeological questions to be asked about the social, cultural and economic roles of these C_4 crops

where they were adopted into pre-existing agricultural systems: for example, in the context of millets' spread into Europe, and the later expansion of maize.

Fortunately, the isotopic differences in C_4 plants compared to C_3 plants discussed above are passed on to the people and animals who consume them (Schwarz 1991). People and animals who consume large quantities of C_4 plants thus have a heavier (less negative) isotopic signature than those who consume solely C_3 plants. Intermediate quantities (or proportions) of C_4 plants in the diet will lead to intermediate isotopic signatures. This isotopic food-chain effect allows C_4 plant consumption to be identified and (semi-) quantified in skeletal remains in the archaeological record (Hedges 2004).

While this basic principle supports a wide range of palaeodietary applications, identifying—and in particular, quantifying—the consumption of C_4 plants is not always straightforward. One problem is that isotope scientists do not have a reliable estimate of the proportion and/or quantity of C_4 foodstuffs that need to be consumed in order for it to be identifiable in skeletal stable carbon isotope values. Addressing this issue is complex because the majority of palaeodietary isotope studies are carried out on bone collagen, which is the primary protein in bone. The body mainly builds protein from amino acids taken directly from protein in the diet; however, some amino acids can be constructed using carbon from non-protein dietary sources (Schwarz 1991). Consequently, bone collagen is biased towards, but not solely reflective of, the protein component of the diet. Isotope scientists tend to estimate that 20 per cent of the protein in the diet needs to originate from a different isotopic source (i.e. 20 per cent C_4 protein in an otherwise C_3 diet) in order for it to be identifiable in bone-collagen isotope ratios (Hedges 2004); however, it is likely that the proportion required to be visible isotopically depends upon a wide range of variables, including health and physiological status; the proportion of protein in the diet; the quality (in terms of amino acid distribution) of that protein; and the amount of food being consumed (Ambrose & Norr 1993; Jim *et al.* 2006; Podlesak & McWilliams 2006). Overall, however, given that plants tend to contain relatively little protein compared to animal products, small amounts of C_4 plant consumption within an omnivorous human diet may be difficult to identify.

Having said that, when C_4 plants are grown or gathered, it is likely that human diets will contain a mixture of C_4 plants and animal products from animals that themselves consumed (varying quantities of) C_4 plants. In this scenario, the consumption of C_4 -fed animal products may mask or confound any

evidence of direct C₄ plant consumption (assuming that the latter is the primary interest). It is therefore necessary to analyse both human and animal bone collagen carbon isotope ratios in order to disentangle direct human C₄ plant consumption, animal C₄ plant consumption and a mixture of the two. This relies on comparing the difference in $\delta^{13}\text{C}$ values between consumer and consumed, and determining whether the difference is notably greater or lesser than would be expected for a trophic level enrichment (i.e. the expected difference in carbon isotope values between consumer and consumed, a value which is itself poorly defined and likely variable).

Alternatively, archaeological scientists can minimize some of the problems inherent in analysing bone collagen by instead analysing the carbon stable isotope ratios of bioapatite (the mineral component of bones and teeth). Bioapatite is in many ways better suited to the identification of C₄ plant consumption, because the carbon in bioapatite reflects the whole diet and includes a higher proportion of carbon from dietary carbohydrate than collagen and other proteins (Ambrose & Norr 1993; Tieszen & Fagre 1993). Because this tissue is not biased towards the protein component of the diet, it is more likely to provide evidence for the consumption of C₄ plants by humans and other omnivores. However, compared with bone collagen, bone apatite is more prone to diagenetic alteration, and for that reason the assessment of carbon in bone apatite is more difficult and contentious. Enamel apatite is less subject to diagenetic alteration, but reflects childhood diet rather than the last years of life. Depending on the archaeological context, a childhood dietary signature may or may not be of archaeological interest. If one does analyse bone or tooth apatite, it is still necessary to analyse animal samples for comparison in order to determine the proportion of C₄ plants and C₄-fed animals in the diet. Where time, samples and finances permit, both bone collagen and (preferably enamel) bioapatite should be analysed in order to provide a complete picture of past diets.

Combining isotopic and archaeobotanical evidence

Both bone collagen and bone bioapatite samples reflect food consumed over a period of years and thus provide an 'averaged' picture of diet (Budd *et al.* 2004; Hedges *et al.* 2007; Stenhouse & Baxter 1979). Their isotopic composition therefore primarily reflects foods that were consumed consistently and in significant quantities over the time represented by the tissue. For this reason, stable isotope scientists often consider only the major crop species (i.e. wheat, barley, rice, the millets, maize, etc.) found archaeobotanically (or assumed based on context) and give less consideration

to edible taxa that are not thought to be major caloric resources in a given diet.

While this approach is not entirely without rationale, the biases associated with archaeological data mean that we have a fragmentary picture of past diets. Even where both archaeobotanical and stable isotope analyses have been carried out, given that both techniques are insensitive to minor dietary components, it is entirely possible that plant species were consumed for which we have little or no archaeological evidence. For example, archaeobotanical preservation of plants consumed by animals is unlikely in contexts where animals were foddered away from the site; any evidence for fodder plants would, in this case, only be present in dung, either because the animal returned to the site within a few days of consumption, or because dung was collected and returned to site to be used as fuel. Similarly, archaeobotanical preservation of human plant foods is unlikely when said species were prepared and eaten beyond the reach of fires. Furthermore, it is difficult to integrate stable isotope and archaeobotanical data directly, as they are biased towards different stages of the subsistence quest; isotopic data reflect food consumption, while archaeobotanical remains are generally thought to reflect food production (e.g. processing remains), although some argue that charred plant remains primarily reflect consumption via fuel—either dung or peat (e.g. Miller 1984; Spengler *et al.* 2013). It is therefore important for the stable isotope scientist to consider all the possible edible C₄ and CAM plants that could have been consumed *by humans or animals* before assuming that any C₄ signal represents only one or two well-known C₄ crops, such as maize and millet. They must also consider that these 'other' C₄ plants could be a single species consumed in relatively high amounts, or a diverse range of species consumed in small quantities by humans and animals, and are likely consumed in conjunction with any available C₄ major crop plants.

The identification of edible C₄ plants for palaeodietary analysis

We argue here for more consideration of the modern edible C₄ and CAM plant species available in the region under study in isotopic palaeodietary analyses: either via a review of previous research or via botanical and/or ethnobotanical surveys if no such work has previously been carried out in the region. Ideally, such studies would centre on the site in question and cover an area large enough to encompass the area exploited by the population of site. In reality, studies' geographical extents will likely be determined by previous botanical research and other such practicalities: this need not preclude useful information being gathered, given that

the aim of such studies is to inform the isotope scientist as to the extent to which they need to consider such plants in their interpretations, rather than to provide an accurate and complete list of the plants consumed.

The two key questions that such studies must address in order to provide a useful platform for palaeodietary analysis are: first, which plants are edible to humans and/or animals; and second, which of those plants use the C_4 or CAM photosynthetic pathway? In the context of a palaeodietary isotope study, where the excavation may well have been completed many years previously and the isotope scientist may never see the site under study, the time and money available for investing in answering these questions is likely limited. Nevertheless, useful data can be derived with minimal effort where ethnobotanical and botanical research has already been undertaken. Where such studies have not been carried out, a more substantial research input may be required, but again we seek to show that this need not be unduly onerous in many cases.

The first question, ‘which plants are edible?’, can often be addressed through a literature survey. In the first two case studies below, lists of edible plants were taken from the literature: one from an academic journal and the other from a ‘Flora’. For the palaeodietary isotope scholar, the limitation of this approach is that one is reliant upon the quality of this previous research. Where such data are unavailable or clearly insufficient, the alternative approach is to undertake an ethnobotanical study personally, likely collaborating with colleagues in other disciplines (for example, botany and social anthropology). Given enough time and resources this is entirely feasible for the palaeodietary isotope scientist, as shown by our third case study below (Cadwallader *et al.* 2012), but requires an investment of time, money and training that is unlikely to be within the scope of most studies. Nevertheless, where a scholar’s research agenda is focused on a particular region, such a study will pay dividends throughout their research career, with all subsequent palaeodietary analyses, as well as their thinking about the past, informed by the plant survey. A final point is that both approaches suffer from the limitation that the plant species currently growing in a region will be an imperfect reflection of the past, and that lists of edible plants are in reality lists of ‘plants recognized as edible’, and may exclude plants that are not currently known to be edible to the local people and/or the researchers involved. Nevertheless, if the aim of the study is to provide an assessment of the general level of edible C_4 and CAM plants available for human and/or animal consumption, such limitations are acceptable, provided that the resulting lists are not biased towards or against one type of photosynthetic pathway.

The second question, ‘which plants use the C_4 photosynthetic pathway?’, may also be addressed with a desk-based literature review as the most convenient starting point. Lists of C_4 plants are available for some regions of the world, ranging from Europe (Collins & Jones 1985) to Aldabra Atoll (Hnatiuk 1980) and including desert regions in India and China (Sankhla *et al.* 1975; Su *et al.* 2011). In such instances, a comparison of a list of C_4 plants and a list of edible plants in a region is simple. Where lists of C_4 species are not available, but a list of edible plants has been acquired, determining which species are C_4 is also relatively straightforward. Firstly, only 17 families contain C_4 species (Acanthaceae, Aizoaceae, Amaranthaceae, Asteraceae, Boraginaceae, Cappariaceae, Caryophyllaceae, Cyperaceae, Euphorbiaceae, Hydrocharitaceae, Molluginaceae, Nyctaginaceae, Poaceae, Polygonaceae, Portulacaceae, Scrophulariaceae and Zygophyllaceae: Simpson 2010) and 35 families contain CAM species (Simpson 2010)—plants in other families can be excluded. Within these families more research must be undertaken. Again, much of this work has already been carried out by scholars in other disciplines and most authors assume that all species within a genus use the same photosynthetic pathway, unless there is evidence to the contrary (Osborne *et al.* 2014). Furthermore, for the Poaceae or grass family (which includes almost half of the world’s C_4 species: Sage *et al.* 1999) a searchable database is available which includes information on each taxon’s photosynthetic pathway (see Osborne *et al.* 2014 for details). For the remaining species, one must search for published papers which have determined the photosynthetic pathway of the species (or, if necessary, genus) under question. There are provisos with this: for example, it is important to ensure that the correct nomenclature is being used, as there are many more recorded scientific names than there are accepted species of grasses (Osborne *et al.* 2014). Nevertheless, if the aim is to attain a general level of understanding of the proportion of edible C_4 plant taxa in the environment, such errors are acceptable, provided that they are acknowledged and that there is no systematic bias.

Where edible plant lists contain many species for which no previous research into their photosynthetic pathway has been undertaken, it may be necessary to study plant samples directly from modern communities: either by analysing their $\delta^{13}C$ values, or by assessing their photosynthetic physiology. The methodology for the former is straightforward, requiring that the plant be dried (or freeze-dried), ground, weighed and then analysed in an isotope-ratio monitoring mass spectrometer. If field sampling is not feasible (for example, due to import/export constraints), it

may be possible to collaborate with institutions such as herbaria and botanic gardens in the researcher's country to obtain samples of edible plants for analysis.

These methods will now be demonstrated through a consideration of edible C₄ plant availability in three regions: Sicily, Italy; Haryana, India; and the south coast of Peru. These regions were chosen to reflect different environmental conditions and to illustrate different methodological approaches to the problem of identifying the diversity of edible C₄ and CAM taxa available.

Sicily, Italy

The first case study is from Sicily, a region where one would expect the proportion of C₄ plants in the environment to be very low. Indeed, research suggests that between 2 and 2.5 per cent of the plant species are C₄ (Collins & Jones 1985), although the proportion of edible C₄ and CAM plants may vary compared to this. A published list of European C₄ plants contains 116 species (Collins & Jones 1985).

Licata and colleagues (2016) conducted a series of interviews with elderly residents in four national parks in Sicily. In total 802 people were interviewed and asked about wild plant food consumption, cooking and cultivation. A total of 119 wild plant foods were identified as being or having been used by the residents. We then compared this list to the list of European C₄ plants in Collins and Jones (1985).

Of the 119 wild plant foods identified by Licata and colleagues (2016), only one (common purslane, *Portulaca oleracea*) appeared on the list of European C₄ species (note that spot checks using the references utilized for Haryana, below, corroborated this finding). In addition, one CAM plant (Indian fig opuntia, *Opuntia ficus-indica*) was identified using a literature search (Ting 1989). Licata and colleagues (2016) also report the Cultural Importance Index for each species (which is a quantitative way to estimate the extent to which each species is present in the local culture and in the memory of the inhabitants), with *Portulaca oleracea* having a value of 0.08 and *Opuntia ficus-indica* a value of 0.19 (for all the plant species, the range of Cultural Importance Index values was from 0.004 to 0.50, with an average value of 0.08).

The data from Sicily therefore show that the number of wild C₄ and CAM plants recognized as edible by Sicilians today is very low. While this list does not include plant species eaten by animals but not humans, it seems reasonable to conclude that any consumption of C₄ or CAM species by humans would be insignificant and likely impossible to identify by stable isotope analysis of either bone collagen or bioapatite (even in the absence of C₄ crops). This

is reassuring and corroborates assumptions made by isotope scientists working in Sicily and the Mediterranean (e.g. Tafuri *et al.* 2009).

Haryana, India

We turn next to Haryana in northwest India. Haryana has three broad topographic zones—a mountainous tract, alluvial plains and sand-dunes—and a large part of the state is arid or semi-arid. Archaeologically, Haryana is notable as having sites dating to the Indus period (e.g. Shinde *et al.* 2008; Singh *et al.* 2011; Wright 2010). To date, limited carbon-isotope analyses have been carried out on skeletal Indus period samples from northwest India; however, even within the limited literature available, the assumption that a C₄ signal represents millet consumption can be found (Chase *et al.* 2014, millet species not specified). This may be true, but is impossible to verify without an assessment of edible C₄ plants in each eco-zone within the Indus region. Here we focus on Haryana due to our on-going research in this region (e.g. Petrie *et al.* 2017).

The *Flora of Haryana* (Kumar 2001) contains a table listing 146 plant species as being edible or used for fodder.¹ However, the individual species information included comments on the consumption of other plants that were not included in the table. These plants were added to the edible plant list, bringing the total to 256 plant species that are eaten by humans or animals today.² From this list, 108 species belong to the families known to contain C₄ or CAM species (see Simpson 2010) and were selected for further study (Table 14.1). Thirty-four of these species were Poaceae and their photosynthetic pathway was determined by searching the Kew taxonomy and photosynthetic pathway database using *Taxonomie* (Kluyver & Osborne 2013; Osborne *et al.* 2014). A literature review was undertaken to determine the photosynthetic pathway of the remaining 74 plant species (references in Table 14.1).

Of the original list of 256 edible plant species, 33 were determined to use the C₄ photosynthetic pathway and 2 utilize the CAM pathway. The photosynthetic pathway could not be determined for 10 species. Thus 13 per cent of edible or fodder species are C₄ and 1 per cent CAM (see Table 14.1). While this proportion of C₄ and CAM plants is relatively small, it is large enough to require consideration in palaeodietary analyses, particularly where human or animal stable carbon-isotope values indicate that C₄ plants (or animals consuming C₄ plants) formed a small proportion of the diet. In such circumstances, it may not be possible to distinguish between the consumption of, in this case, millet species and the consumption of one or more other C₄ plants.

Table 14.1. List of edible plants found in Haryana (derived from Kumar 2001) and their photosynthetic pathways.

Species	Family	Pathway	Reference for photosynthesis
<i>Peristrophe bicalyculata</i>	Acanthaceae	C ₃	Sankhla <i>et al.</i> 1975
<i>Amaranthus roxburghianus</i>	Amaranthaceae	C ₃	Liu & Wang 2006
<i>Deeringia amaranthoides</i>	Amaranthaceae	C ₃	Sage <i>et al.</i> 2007
<i>Digera muricata</i>	Amaranthaceae	C ₃	Sage <i>et al.</i> 2007; Sankhla <i>et al.</i> 1975
<i>Coriandrum sativum</i>	Apiaceae	C ₃	Wulschleger 1993
<i>Cuminum cyminum</i>	Apiaceae		
<i>Daucus carota</i>	Apiaceae		
<i>Foeniculum vulgare</i>	Apiaceae	C ₃	Marchese <i>et al.</i> 2006
<i>Pimpinella involucrata</i>	Apiaceae	C ₃	Poorter <i>et al.</i> 1990
<i>Carissa congesta</i>	Apocyanaceae		
<i>Carissa spinarum</i>	Apocyanaceae	C ₃	Zhang <i>et al.</i> 2007
<i>Vallis solanacea</i>	Apocyanaceae		
<i>Amorphophallus campanulatus</i>	Araceae	C ₃	Ravi <i>et al.</i> 2009
<i>Colocasia esculenta</i>	Araceae	C ₃	Wulschleger 1993
<i>Carthamus oxyacantha</i>	Asteraceae	C ₃	Khaki-Moghadam & Rokhzadi 2015
<i>Centipeda minima</i>	Asteraceae	C ₃	Liu & Wang 2006
<i>Cichorium intybus</i>	Asteraceae	C ₃	Saini <i>et al.</i> 2011
<i>Helianthus annuus</i>	Asteraceae	C ₃	Wulschleger 1993
<i>Lactuca sativa</i>	Asteraceae	C ₃	Brownwell & Crossland 1972
<i>Oligochaeta ramosa</i>	Asteraceae	C ₃	Sankhla <i>et al.</i> 1975
<i>Sonchus asper</i>	Asteraceae	C ₃	Sankhla <i>et al.</i> 1975
<i>Sonchus brachyotus</i>	Asteraceae	C ₃	Sankhla <i>et al.</i> 1975
<i>Sonchus oleraceus</i>	Asteraceae	C ₃	Sankhla <i>et al.</i> 1975
<i>Ehretia acuminata</i>	Boraginaceae	C ₃	Sankhla <i>et al.</i> 1975
<i>Ehretia aspera</i>	Boraginaceae	C ₃	Sankhla <i>et al.</i> 1975
<i>Trichodesma amplexicaule</i>	Boraginaceae	C ₃	Sankhla <i>et al.</i> 1975; Ziegler <i>et al.</i> 1981
<i>Opuntia dillenii</i>	Cactaceae	CAM	Ting 1989
<i>Opuntia elatior</i>	Cactaceae	CAM	Winter <i>et al.</i> 2011
<i>Capparis decidua</i>	Capparaceae	C ₃	Sankhla <i>et al.</i> 1975
<i>Capparis zeylanica</i>	Capparaceae	C ₃	Hnatiuk 1980
<i>Sueda fruticosa</i>	Chenopodiaceae	C ₄	Malik <i>et al.</i> 1991
<i>Beta vulgaris</i>	Chenopodiaceae	C ₃	Wulschleger 1993
<i>Kochia indica</i>	Chenopodiaceae	C ₄	Malik <i>et al.</i> 1991
<i>Spinacea oleracea</i>	Chenopodiaceae	C ₃	Crawford <i>et al.</i> 1986
<i>Ipomoea eriocarpa</i>	Convolvulaceae	C ₃	Hnatiuk 1980
<i>Benincasa hispida</i>	Cucurbitaceae		
<i>Citrullus fistulosus</i>	Cucurbitaceae	C ₃	Sankhla <i>et al.</i> 1975
<i>Citrullus lanatus</i>	Cucurbitaceae	C ₃	Akashi <i>et al.</i> 2011
<i>Cucumis melo</i>	Cucurbitaceae	C ₃	Govindachary <i>et al.</i> 2007
<i>Cucumis melo</i> var. <i>momordica</i>	Cucurbitaceae	C ₃	Govindachary <i>et al.</i> 2007
<i>Cucumis melo</i> var. <i>utilissimus</i>	Cucurbitaceae	C ₃	Govindachary <i>et al.</i> 2007
<i>Cucurbita maxima</i>	Cucurbitaceae	C ₃	Llano 2008
<i>Cucurbita pepo</i>	Cucurbitaceae	C ₃	Rintamaki <i>et al.</i> 1988
<i>Lagenaria siceraria</i>	Cucurbitaceae	C ₃	Tankersley <i>et al.</i> 2016
<i>Luffa acutangula</i>	Cucurbitaceae	C ₃	Cadwallader <i>et al.</i> 2012

Table 14.1. (Continued.)

Species	Family	Pathway	Reference for photosynthesis
<i>Luffa aegyptiaca</i>	Cucurbitaceae	C ₃	Cadwallader <i>et al.</i> 2012
<i>Luffa cylindrica</i>	Cucurbitaceae	C ₃	Cadwallader <i>et al.</i> 2012
<i>Momordica charantia</i>	Cucurbitaceae	C ₃	Lin <i>et al.</i> 1986
<i>Momordica dioica</i>	Cucurbitaceae	C ₃	Cadwallader <i>et al.</i> 2012
<i>Trichosanthes anguina</i>	Cucurbitaceae		
<i>Trichosanthes dioica</i>	Cucurbitaceae		
<i>Carex fedia</i>	Cyperaceae	C ₄	Smith & Epstein 1971
<i>Diospyros exculpta</i>	Ebenaceae	C ₃	Lancelotti <i>et al.</i> 2013
<i>Phyllanthus emblica</i>	Euphorbiaceae	C ₃	Sankhla <i>et al.</i> 1975; Hnatiuk 1980
<i>Ricinus communis</i>	Euphorbiaceae	C ₃	Wullschleger 1993; Ziegler <i>et al.</i> 1981
<i>Sapium maritimus</i>	Euphorbiaceae		
<i>Securinega leucopyrus</i>	Euphorbiaceae		
<i>Vallisneria spiralis</i>	Hydrocharitaceae	C ₃	Hough & Wetzel 1977
<i>Ocimum sanctum</i>	Lamiaceae	C ₃	Marchese <i>et al.</i> 2006
<i>Gisekia pharnaceoides</i>	Molluginaceae	C ₄	Seenii & Gnanam 1983
<i>Moringa oleifera</i>	Moringaceae	C ₃	Hnatiuk 1980
<i>Moringa pterigosperma (oleifera)</i>	Moringaceae	C ₃	Hnatiuk 1980
<i>Oxalis corniculata</i>	Oxalidaceae	C ₃	Liu & Wang 2006
<i>Arachne racemosa</i>	Poaceae	C ₄	<i>Taxonome</i> (Kluyver & Osborne 2013; Osborne <i>et al.</i> 2014)
<i>Aristida funiculata</i>	Poaceae	C ₄	<i>Taxonome</i> (Kluyver & Osborne 2013; Osborne <i>et al.</i> 2014)
<i>Avena fatua</i>	Poaceae	C ₃	<i>Taxonome</i> (Kluyver & Osborne 2013; Osborne <i>et al.</i> 2014)
<i>Avena sterilis</i>	Poaceae	C ₃	<i>Taxonome</i> (Kluyver & Osborne 2013; Osborne <i>et al.</i> 2014)
<i>Cenchrus biflorus</i>	Poaceae	C ₄	<i>Taxonome</i> (Kluyver & Osborne 2013; Osborne <i>et al.</i> 2014)
<i>Cenchrus prieurii</i>	Poaceae	C ₄	<i>Taxonome</i> (Kluyver & Osborne 2013; Osborne <i>et al.</i> 2014)
<i>Cenchrus setigerus</i>	Poaceae	C ₄	<i>Taxonome</i> (Kluyver & Osborne 2013; Osborne <i>et al.</i> 2014)
<i>Chloris dolichostachya</i>	Poaceae	C ₄	<i>Taxonome</i> (Kluyver & Osborne 2013; Osborne <i>et al.</i> 2014)
<i>Chrysopogon fulvus</i>	Poaceae	C ₄	<i>Taxonome</i> (Kluyver & Osborne 2013; Osborne <i>et al.</i> 2014)
<i>Cymbopogon jwarancusa</i>	Poaceae	C ₄	<i>Taxonome</i> (Kluyver & Osborne 2013; Osborne <i>et al.</i> 2014)
<i>Cymbopogon schoenanthus</i>	Poaceae	C ₄	<i>Taxonome</i> (Kluyver & Osborne 2013; Osborne <i>et al.</i> 2014)
<i>Cynodon dactylon</i>	Poaceae	C ₄	<i>Taxonome</i> (Kluyver & Osborne 2013; Osborne <i>et al.</i> 2014)
<i>Dichanthium annulatum</i>	Poaceae	C ₄	<i>Taxonome</i> (Kluyver & Osborne 2013; Osborne <i>et al.</i> 2014)
<i>Echinochloa colona</i>	Poaceae	C ₄	<i>Taxonome</i> (Kluyver & Osborne 2013; Osborne <i>et al.</i> 2014)
<i>Echinochloa crusgalli</i>	Poaceae	C ₄	<i>Taxonome</i> (Kluyver & Osborne 2013; Osborne <i>et al.</i> 2014)
<i>Eleusine coracana</i>	Poaceae	C ₄	<i>Taxonome</i> (Kluyver & Osborne 2013; Osborne <i>et al.</i> 2014)
<i>Eleusine indica</i>	Poaceae	C ₄	<i>Taxonome</i> (Kluyver & Osborne 2013; Osborne <i>et al.</i> 2014)
<i>Eragrostis cilianensis</i>	Poaceae	C ₄	<i>Taxonome</i> (Kluyver & Osborne 2013; Osborne <i>et al.</i> 2014)
<i>Hordeum vulgare</i>	Poaceae	C ₃	<i>Taxonome</i> (Kluyver & Osborne 2013; Osborne <i>et al.</i> 2014)
<i>Lasiurus scindicus</i>	Poaceae	C ₄	<i>Taxonome</i> (Kluyver & Osborne 2013; Osborne <i>et al.</i> 2014)
<i>Oryza sativa</i>	Poaceae	C ₃	<i>Taxonome</i> (Kluyver & Osborne 2013; Osborne <i>et al.</i> 2014)
<i>Panicum antidotale</i>	Poaceae	C ₄	<i>Taxonome</i> (Kluyver & Osborne 2013; Osborne <i>et al.</i> 2014)
<i>Panicum astrosanguinem</i>	Poaceae	C ₄	<i>Taxonome</i> (Kluyver & Osborne 2013; Osborne <i>et al.</i> 2014)
<i>Panicum paludosum</i>	Poaceae	C ₄	<i>Taxonome</i> (Kluyver & Osborne 2013; Osborne <i>et al.</i> 2014)
<i>Panicum trypheron</i>	Poaceae	C ₄	<i>Taxonome</i> (Kluyver & Osborne 2013; Osborne <i>et al.</i> 2014)
<i>Pennisetum typhoides</i>	Poaceae	C ₄	<i>Taxonome</i> (Kluyver & Osborne 2013; Osborne <i>et al.</i> 2014)
<i>Phalaris minor</i>	Poaceae	C ₃	<i>Taxonome</i> (Kluyver & Osborne 2013; Osborne <i>et al.</i> 2014)

Table 14.1. (Continued.)

Species	Family	Pathway	Reference for photosynthesis
<i>Saccharum officinarum</i>	Poaceae	C ₄	<i>Taxonomie</i> (Kluyver & Osborne 2013; Osborne <i>et al.</i> 2014)
<i>Setaria glauca</i>	Poaceae	C ₄	<i>Taxonomie</i> (Kluyver & Osborne 2013; Osborne <i>et al.</i> 2014)
<i>Setaria pumila</i>	Poaceae	C ₄	<i>Taxonomie</i> (Kluyver & Osborne 2013; Osborne <i>et al.</i> 2014)
<i>Setaria verticillata</i>	Poaceae	C ₄	<i>Taxonomie</i> (Kluyver & Osborne 2013; Osborne <i>et al.</i> 2014)
<i>Sorghum vulgare</i>	Poaceae	C ₄	<i>Taxonomie</i> (Kluyver & Osborne 2013; Osborne <i>et al.</i> 2014)
<i>Triticum aestivum</i>	Poaceae	C ₃	<i>Taxonomie</i> (Kluyver & Osborne 2013; Osborne <i>et al.</i> 2014)
<i>Zea mays</i>	Poaceae	C ₄	<i>Taxonomie</i> (Kluyver & Osborne 2013; Osborne <i>et al.</i> 2014)
<i>Fagopyrum esculentum</i>	Polygonaceae	C ₃	Liu & Wang 2006
<i>Rumex vesicarius</i>	Polygonaceae	C ₃	Raghavendra & Das 1978
<i>Borreria articularis</i>	Rubiaceae	C ₃	Ziegler <i>et al.</i> 1981
<i>Mitragyna parvifolia</i>	Rubiaceae	C ₃	Bidalia <i>et al.</i> 2017
<i>Morinda tomentosa</i>	Rubiaceae		
<i>Euphoria longana</i>	Sapindaceae	C ₃	Weng & Lai 2003
<i>Litchi chinensis</i>	Sapindaceae	C ₃	Hieke <i>et al.</i> 2002
<i>Scoparia dulcis</i>	Scrophulariaceae	C ₃	Yoneyama <i>et al.</i> 2010
<i>Dodonaea viscosa</i>	Vitaceae	C ₃	Rao <i>et al.</i> 1979
<i>Vitis vinifera</i>	Vitaceae	C ₃	Wullschleger 1993
<i>Zygophyllum simplex</i>	Zygophyllaceae	C ₄	Ziegler <i>et al.</i> 1981

South coast of Peru

Our third case study (Cadwallader *et al.* 2012) uses ethnobotanical research combined with field collection and herbarium specimens to consider C₄ and CAM food sources on the south coast of Peru. This is a region where maize has played an important social role with ritual significance, as well as being the main staple crop by the Inca Late Horizon period (Godelier 1977; Goldstein 2003; Hastorf & Johannessen 1993; Isbell 1988; Valdez 2006). As such, maize consumption has been well studied isotopically (e.g. Burger & van der Merwe 1990; Kellner & Schoeninger 2008), but, until recently, relatively few of these works consider other C₄ plant sources in the human diet.

Cadwallader and colleagues (2012) conducted an ethnobotanical study to determine which plants were likely consumed by humans or animals; this included talking to local llama herders (Cadwallader pers. comm., 2017), as well as referring to published works. On this basis 89 species were selected for isotopic analysis. Samples of these species were then collected either from the field or from the Herbarium at the Royal Botanic Gardens Kew, UK. The samples were dried, ground, weighed and analysed in a mass spectrometer (refer to Cadwallader *et al.* 2012 for full details).

Of the 89 species analysed, 40 were found to use the C₃ photosynthetic pathway, 38 used the C₄ photosynthetic pathway and the remaining 2 used CAM photosynthesis. The authors combined these new

data with published studies from regions with similar ecologies, creating a synthesized dataset containing 144 different plant species (cf. DeNiro & Hastorf 1985; Tieszen & Chapman 1992). Of these, 96, 41 and 7 plant species use the C₃, C₄ and CAM photosynthetic pathways, respectively.

This study demonstrates that a third of the plants analysed from the south coast of Peru utilized the C₄ or CAM photosynthetic pathway. Clearly, this is hugely significant for the identification of maize consumption in the archaeological record and arguably undermines many of the previous palaeodietary studies in the region. Under such circumstances it is not advisable to equate a human or animal carbon-isotope value directly with a single crop, as there could well be a substantial contribution from other C₄ and CAM plant species. Many studies in the Andean region are now recognizing that maize may not be the only explanation for high human $\delta^{13}\text{C}$ values, and this has led to an improved and more nuanced understanding of the past (e.g. Marstella *et al.* 2016). Nevertheless, the idea that C₄ signals equal maize consumption persists in the literature.

Where does this leave us?

None of the above approaches allows a definitive determination of which edible C₄ and CAM plants were available in the past, particularly in the context of shifting distributions, nor do these approaches

comment upon whether plants that are recognized as edible today were actually consumed in the past. In particular, there is a risk of excluding plants that are no longer consumed by populations today, as exemplified by a number of indigenous American ‘lost crops’, once consumed regularly, but which have now largely or entirely fallen out of use (Mueller *et al.* 2017). Nevertheless, despite these limitations, the types of studies proposed here provide a relatively simple means for a more nuanced consideration of past diets. By conducting such studies, isotope scientists can better understand the extent to which C₄ and CAM plants other than the major crop species must be considered in their interpretations.

In situations such as Sicily, where only one edible C₄ and one edible CAM plant were found, it is reasonable to interpret any evidence for C₄ consumption in skeletal stable isotope values as the consumption of the appropriate C₄ crop. In prehistoric Europe this equates to one or more millet species, with maize another possible interpretation in more recent samples. Interpreting human and animal isotope data in contexts such as the southern coast of Peru is more challenging, given that approximately a third of the edible plants available use the C₄ or CAM photosynthetic pathways. In this area, a small enrichment in $\delta^{13}\text{C}$ values compared to that which would be expected for an entirely C₃-based diet may relate either to the consumption of maize or the consumption of other edible C₄ and CAM plants, or both. A careful consideration of the archaeobotanical data, and the use of multiple tissues from both human and animal remains, may shed more light on this problem (e.g. Cadwallader *et al.* 2012), but given the limitations of both archaeobotany and stable isotope analysis, it is likely to be impossible to exclude the consumption of C₄ and CAM plants other than maize in the past.

Compared to Sicily, where C₄ consumption is *unlikely* to include C₄ plants other than major crop species, or to the south coast of Peru, where C₄ consumption is *likely* to include C₄ plants other than major crop species, situations such as those in Haryana are perhaps more frustrating. Our study shows that edible C₄ and CAM species other than (various) millets are currently available; however, the proportion of these plants is intermediate between the negligible proportion available in Sicily and the notable proportion available in Peru. The interpretation of human and animal stable carbon isotope results is therefore problematic—while it is conceivable that many C₄ or CAM species were eaten by animals and/or humans, it is equally conceivable that only (various species of) millet were consumed in notable amounts. Without evidence from other sources (such as dung; Qiu *et al.*

2014), it may not be possible to distinguish between these two scenarios. While this does not preclude stable isotopic data from contributing to hypotheses and models of past human food systems, the degree of uncertainty that remains must be fully acknowledged.

Conclusion

Ultimately, stable carbon-isotope analysis of skeletal remains distinguishes between photosynthetic pathways (ignoring the potential confounding factor of aquatic resource consumption: see e.g. Bogaard & Outram 2013); it does not comment on the species of plant consumed. The interpretation of skeletal $\delta^{13}\text{C}$ values thus involves one or more assumptions based on varying amounts of supporting evidence. Any scientific interpretation is only as strong as the assumptions on which it is based, and testing those assumptions is an integral part of scientific endeavour. Here, we advocate for further consideration of one of these assumptions—that few edible C₄ (or CAM) plants exist in a region apart from the well-known major crop species. We show that addressing this issue need not be an onerous or expensive undertaking, but recognize that such a study is unlikely to be either completely comprehensive or entirely accurate. Nevertheless, on a general level, this approach serves to inform isotope scientists and other archaeologists of the potential for the consumption of C₄ and CAM plants other than the major crop species and thus helps to provide a more accurate, comprehensive and nuanced understanding of past diets and subsistence practices.

Notes

1. No plants were excluded from the analysis on the basis of their likely origin: e.g. maize is included on the list in Table 14.1.
2. Only plants explicitly noted as being eaten were included; medicinal plants, weeds and plants only described as cultivated were not included.

Appreciation and acknowledgements

All authors would like to thank past and present members of the Dorothy Garrod and George Pitt-Rivers laboratories for thought-provoking discussions over many years.

Martin Jones has played a pivotal role in the careers of all three authors, supervised all of our PhDs at one time or another and written us many, many references. It is fair to say that none of us would be where we are today without his help and guidance. Thank you, Martin.

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